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## IDENTICAL METABOLIC RATE AND THERMAL CONDUCTANCE IN ROCK SANDPIPER (*CALIDRIS PTILOCNEMIS*) SUBSPECIES WITH CONTRASTING NONBREEDING LIFE HISTORIES

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**ABSTRACT.**—Closely related species or subspecies can exhibit metabolic differences that reflect site-specific environmental conditions. Whether such differences represent fixed traits or flexible adjustments to local conditions, however, is difficult to predict across taxa. The nominate race of Rock Sandpiper (*Calidris ptilocnemis*) exhibits the most northerly nonbreeding distribution of any shorebird in the North Pacific, being common during winter in cold, dark locations as far north as upper Cook Inlet, Alaska (61°N). By contrast, the *tschuktschorum* subspecies migrates to sites ranging from about 59°N to more benign locations as far south as ~37°N. These distributional extremes exert contrasting energetic demands, and we measured common metabolic parameters in the two subspecies held under identical laboratory conditions to determine whether differences in these parameters are reflected by their nonbreeding life histories. Basal metabolic rate and thermal conductance did not differ between subspecies, and the subspecies had a similar metabolic response to temperatures below their thermoneutral zone. Relatively low thermal conductance values may, however, reflect intrinsic metabolic adaptations to northerly latitudes. In the absence of differences in basic metabolic parameters, the two subspecies' nonbreeding distributions will likely be more strongly influenced by adaptations to regional variation in ecological factors such as prey density, prey quality, and foraging habitat. Received 19 April 2012, accepted 4 September 2012.

**Key words:** basal metabolic rate, BMR, *Calidris ptilocnemis*, metabolic rate, phenotypic flexibility, Rock Sandpiper, shorebirds, temperature effects, thermal conductance.

### La Tasa Metabólica y la Conductancia Térmica son Idénticas en Subespecies de *Calidris ptilocnemis* con Historias Contrastantes de Vida No Reproductiva

**RESUMEN.**—Las especies cercanamente relacionadas o subespecies pueden exhibir diferencias metabólicas que reflejan las condiciones ambientales específicas de cada sitio. Sin embargo, es difícil predecir a través de varios taxones si tales diferencias representan rasgos fijados o ajustes flexibles a las condiciones locales. La raza nominal de *Calidris ptilocnemis* tiene la distribución no reproductiva más septentrional entre las aves playeras del Pacífico Norte, siendo común durante el invierno en localidades frías y oscuras como Cook Inlet, Alaska (61°N). En contraste, la subespecie *tschuktschorum* migra hacia sitios que desde los 59°N hasta localidades más benignas hacia el sur alrededor de 37°N. Estos extremos en la distribución ejercen demandas energéticas contrastantes. Medimos parámetros metabólicos comunes en ambas subespecies mantenidas bajo condiciones de laboratorio idénticas para determinar si las diferencias en estos parámetros se ven reflejadas en sus historias de vida no reproductiva. La tasa metabólica basal y la conductancia térmica no fueron diferentes entre subespecies, y éstas presentaron una respuesta metabólica similar a temperaturas por debajo de su zona termoneutral. Sin embargo, valores relativamente bajos de conductancia térmica podrían reflejar adaptaciones metabólicas intrínsecas a latitudes más altas. En la ausencia de diferencias en las tasas metabólicas basales, probablemente las distribuciones no reproductivas de las dos subespecies podrían verse más fuertemente influenciadas por adaptaciones a la variación regional en factores ecológicos como la densidad y calidad de las presas y los sitios de forrajeo.

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LIFE HISTORY TRAITS are ultimately determined by an organism's genotype (Stearns 1989), but environmental conditions strongly shape the phenotypic expression of genetic traits (Piersma and van Gils 2011). Comparisons between closely related species, subspecies, or populations with divergent life-history traits can help discern the contributions of genes and environment in determining basic metabolic and physiological variables (Mueller and Diamond 2001, Wikelski et al. 2003). Previous comparisons across a wide array of taxa have investigated a variety of physiological parameters, including metabolic rate (Klaassen 1995, Piersma 1996), immune response (Buehler et al. 2009), total evaporative water loss (Williams et al. 2004, Tieleman 2007), growth rate (Niewiarowski and Roosenburg 1993), digestive function (Mueller and Diamond 2001; van Gils et al. 2005a, b), and thermal conductance (Scholander et al. 1950a, b). Despite numerous studies, however, no predictable patterns have emerged to show how phenotypically flexible traits are modulated across taxa.

As a group, shorebirds in the family Scolopacidae lend themselves to such comparisons because of their diverse life histories (e.g., Pitelka et al. 1974, Piersma 2007) and discrete genetic lineages within species (e.g., Buehler and Baker 2005). Members of this family tend to breed at relatively high latitudes and are highly migratory, most conducting annual migrations totaling 10,000–30,000 km between high-latitude breeding grounds and temperate nonbreeding locations (Piersma et al. 1996b, Battley et al. 2012). Migratory shorebirds exhibit considerable phenotypic flexibility that enables efficient physiological “retooling” to accommodate these migratory behaviors (Piersma and Lindström 1997, Battley and Piersma 2005). For scolopacid shorebirds, a less-common life-history strategy involves staying at or near high-latitude breeding sites throughout the year, but physiological adaptations to this life-history strategy are comparatively little studied. Such a strategy is predicted to also involve great physiological change, including elevated metabolic rates (Weathers 1979, Piersma et al. 1996a), increased lipid stores (White and West 1977, Blem 1990), improved insulative capacities (Dawson and Carey 1976, Carey et al. 1978), and increased digestive and metabolic efficiencies (Dykstra and Karasov 1992, Karasov 1996).

In the North Pacific Basin, the Rock Sandpiper (*Calidris ptilocnemis*) is the shorebird species with the most northerly nonbreeding distribution (Gill et al. 2002). Four subspecies of Rock Sandpiper are recognized on the basis of appearance and

morphology (Conover 1944) and genetic analyses (Pruett and Winker 2005), and the subspecies exhibit differential migration patterns. Two subspecies (*C. p. couesi* and *C. p. quarta*) are essentially nonmigratory, moving primarily between upland breeding sites and coastal nonbreeding sites. A third (*C. p. ptilocnemis*) moves relatively short distances ( $\leq 1,500$  km) between breeding and nonbreeding sites, and the fourth subspecies (*C. p. tschuktschorum*) migrates longer distances ( $\sim 4,000$  km; Gill et al. 2002).

Because of migratory propensity and prevailing environmental conditions, the nonbreeding distributions of *C. p. ptilocnemis* and *C. p. tschuktschorum* represent the life-history extremes for the species. *Calidris p. ptilocnemis* (hereafter *ptilocnemis*) spends the nonbreeding season primarily in upper Cook Inlet, Alaska (61°N, 151°W; Ruthrauff et al. 2013), a site with expansive mudflats and abundant food resources. In the winter, the mean daily temperature in this region is  $<0^{\circ}\text{C}$  for nearly 5 months from November to March; consequently, the upper intertidal zone in Cook Inlet accretes with thick sea ice, and critical mudflat habitats become less accessible as the winter progresses (Ruthrauff et al. 2013). By contrast, *C. p. tschuktschorum* (hereafter *tschuktschorum*) is distributed along the eastern North Pacific coast from about 59° to 37°N in winter (Gill et al. 2002). The distribution and population structure of *tschuktschorum* across this range are unknown, but in general, *tschuktschorum* individuals less commonly encounter temperatures  $<0^{\circ}\text{C}$ , rarely experience ice coverage of preferred rocky intertidal foraging habitats, and exploit longer day lengths than in upper Cook Inlet. Although the subspecies probably co-occur in small numbers at their distributional extremes, their winter distributions are largely non-overlapping.

Latitudinal gradients in environmental conditions at these nonbreeding sites exert contrasting energetic demands. Applying long-term meteorological data, the predicted average maintenance metabolic rate in December for a hypothetical 85-g *ptilocnemis* in upper Cook Inlet is 2.55 W (Table 1). Given their wider nonbreeding range, similarly derived values for *tschuktschorum* range from 1.64 to 2.43 W for birds wintering at locations representative of the southern (Humboldt Bay, California; 41°N) and northern (Juneau, Alaska; 58°18'N) extents of their nonbreeding range, respectively (Table 1). Thus, the nonbreeding distributions and migratory predispositions of these two subspecies represent extremes not only along a life history continuum, but

TABLE 1. Long-term average environmental conditions in December and resulting predicted energetic demands for Rock Sandpipers wintering at distributional extremes. *Calidris ptilocnemis ptilocnemis* winters primarily in upper Cook Inlet, Alaska, and *C. p. tschuktschorum* is widely distributed along the eastern Pacific coast from 59° to 37°N. Metabolic rates refer to the thermostatic costs (i.e., do not include activity costs) and are calculated following equation 5 in Wiersma and Piersma (1994; values for “solitary bird”), using conductance value  $K_{es} = 0.036$  (Calder 1996).

Site <sup>a</sup>	Latitude	Temperature <sup>b</sup>	Wind <sup>c</sup>	Insolation <sup>d</sup>	Daylight <sup>e</sup>	Predicted metabolic rate <sup>f</sup>
UCI	61°N	−5.3, −12.2, −8.7	2.8	6	5:38	2.55
JUN	58°18'N	−0.2, −5.2, −2.7	4.0	10	6:30	2.43
HUM	41°N	12.7, 5.6, 9.1	2.9	70	9:19	1.64

<sup>a</sup> UCI = upper Cook Inlet, Alaska; JUN = Juneau, Alaska; HUM = Humboldt Bay, California.

<sup>b</sup> High, low, mean ( $^{\circ}\text{C}$ ; Western Regional Climate Center 2012).

<sup>c</sup>  $\text{m s}^{-1}$  (Western Regional Climate Center 2012).

<sup>d</sup>  $\text{W m}^{-2}$  (National Aeronautics and Space Administration 2012).

<sup>e</sup> Hours:minutes (U.S. Naval Observatory 2012).

<sup>f</sup> Watts (following procedures of Wiersma and Piersma 1994).

also along an exercise–physiology continuum. Predicted differences in metabolic rates between the two subspecies (4.7–35.7%) and between *tschuktschorum* at the northern and southern extents of their nonbreeding range (32.5%) speak to the inherent expansibility of metabolic rates in shorebirds (Swanson 2010, Piersma 2011), and metabolic expansibility and summit metabolic rates are related to basic physiological measures like basal metabolic rate (Dutenhoffer and Swanson 1996, Rezende et al. 2002). Differences in predicted metabolic rates could thus be reflected by intrinsic differences in Rock Sandpiper physiological parameters.

We tested this on Rock Sandpipers maintained in a common environment, enabling us to assess the degree to which each subspecies' life history is reflected in inherent differences in basic physiological parameters. Previous studies have demonstrated that birds at colder sites or during colder seasons have lower conductance than those at warmer locations or during warmer seasons (Blem 1981, Cooper 2002). When maintained under similar conditions, increased insulative capacity in one population may enable relatively lower metabolic rates and increased cold resistance compared with another population with a lower insulative capacity (West 1972, Vézina et al. 2009). By virtue of their wintering at locations that require consistently greater metabolic output, we hypothesized that in the absence of metabolic flexibility, *ptilocnemis* would have (1) a higher basal metabolic rate (BMR; the energy consumption of a resting, postabsorptive animal in a normothermic environment; IUPS Thermal Commission 2003), (2) lower metabolic rates at temperatures below their thermoneutral zone, and (3) lower thermal conductance than *tschuktschorum*.

## METHODS

**Experimental animals and maintenance.**—We included 27 adult Rock Sandpipers in the trials, including 15 *ptilocnemis* (7 females, 8 males) and 12 *tschuktschorum* (6 females, 6 males). The birds were captured on 28 August 2009 at a postbreeding site on the Yukon Delta National Wildlife Refuge, Alaska (61°19'N, 165°47'W). We determined the subspecific identity of birds on the basis of diagnostic plumage characteristics of the wing and mantle (Gill et al. 2002), and sex via standard polymerase chain reaction techniques (Griffiths et al. 1996).

We transported the birds to the NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands, on 21 September 2009. Following a 1-month health quarantine period, the birds were randomly assigned to one of three identical outdoor aviaries on 27 October 2009. The birds were exposed to the local ambient temperature and photoperiod at 51°N, but sheltered from wind and precipitation (for aviary details, see Vézina et al. 2006). The mean ( $\pm$  SE) monthly temperatures during the trial period were  $9.6 \pm 0.4^\circ\text{C}$  for November 2009,  $3.4 \pm 0.7^\circ\text{C}$  for December 2009,  $-0.3 \pm 0.4^\circ\text{C}$  for January 2010,  $1.2 \pm 0.5^\circ\text{C}$  for February 2010, and  $5.6 \pm 0.6^\circ\text{C}$  for March 2010, as measured at the Royal Netherlands Meteorological Institute station in De Kooij, North Holland (see Acknowledgments), 8 km south of the NIOZ aviaries.

**Respirometry.**—We randomly assigned birds to metabolic trials on the basis of subspecies and sex, selecting one member of each subspecies of each sex per trial. The first respirometry trial was conducted on 23 November 2009, 27 days after the birds were established in outside aviaries. We measured oxygen consumption

( $V_{O_2}$ ) and calculated metabolic rates using a flow-through respirometry system on  $\leq 4$  individuals per trial (for setup details, see Vézina et al. 2006).

Metabolic chambers were held in a dark, climate-controlled thermocabinet, and birds were maintained overnight from 1600 to 0900 hours during all trials. For the BMR trials, birds were held at  $18^\circ\text{C}$ , a temperature assumed to be within the species' thermoneutral zone on the basis of comparisons to similar shorebirds (e.g., Ruddy Turnstone [*Arenaria interpres*; Kersten and Piersma 1987], Red Knot [*C. canutus*; Piersma et al. 2004], and Sanderling [*C. alba*; Castro 1987]). We conducted one respirometry trial per bird for BMR calculations. After completing the BMR trials, we observed that metabolic rates were consistent across the latter half of each 17-h trial, and so to augment our ability to measure the metabolic response of Rock Sandpipers to temperature (hereafter “temperature trials”), we conducted subsequent trials at two predictive temperatures per trial. Following this protocol, birds were kept at  $18^\circ\text{C}$  for the first 8 h of each temperature trial, and then adjusted to the first predictive temperature for 4 h, followed by a second predictive temperature for another 4 h. After 16 h, the metabolic chambers were once again regulated to  $18^\circ\text{C}$  for a 1-h recovery period. We programmed the temperature trials to minimize temperature fluctuations because severe temperature swings induced locomotor activity that disrupted the birds' resting state and increased oxygen consumption. For similar reasons, we paired each trial's two temperatures to minimize temperature fluctuations (i.e., trials at  $10^\circ\text{C}$  were paired with measurements at  $5^\circ\text{C}$  rather than  $-20^\circ\text{C}$ ). We conducted one respirometry trial per bird for temperature trials in which they were included.

We calculated each bird's metabolic rate over the 10-min period with the lowest  $V_{O_2}$  for all BMR and temperature trials. The mean ( $\pm$  SE) respiratory quotient during the BMR trials was  $0.715 \pm 0.005$ , a value indicative of fat metabolism in a postabsorptive bird (Bartholomew 1982), and so we used an energy conversion value of  $19.8 \text{ kJ l}^{-1} \text{ O}_2$  (Gessaman and Nagy 1988) and converted this value to watts ( $1 \text{ kJ h}^{-1} = 0.277 \text{ W}$ ). Calculations were performed using Sable Systems ExpeData software (Las Vegas, Nevada). Twenty-seven birds were included in the BMR trials, and 26 birds were included in the temperature trials. Because of conflict with concurrent experiments, not all 26 individuals were measured at all temperatures (for sample sizes, see Fig. 1). We measured the metabolic response of 8, 10, and 8 birds at two, three, and six predictive temperatures, respectively. We conducted the BMR trials from 23 to 30 November 2009; trials at  $10^\circ\text{C}$  and  $5^\circ\text{C}$  from 8 to 11 December 2009; trials at  $-5^\circ\text{C}$  and  $-10^\circ\text{C}$  from 13 to 16 December 2009; trials at  $14^\circ\text{C}$  and  $22^\circ\text{C}$  from 26 to 27 February 2010; and trials at  $-15^\circ\text{C}$  and  $-20^\circ\text{C}$  from 5 to 6 March 2010.

**Statistical analyses.**—We fit generalized linear models to assess the effect of relevant biological parameters on the metabolic rate of Rock Sandpipers. We conducted separate analyses for the BMR trials and the temperature trials. For the BMR trials, we modeled the effect of subspecies (*ptilocnemis* or *tschuktschorum*), sex (male or female), and body mass on BMR. We modeled the effect of the aforementioned predictor variables as well as temperature below the lower critical temperature ( $-20^\circ$ ,  $-15^\circ$ ,  $-10^\circ$ ,  $-5^\circ$ ,  $5^\circ$ ,  $10^\circ$ , and  $14^\circ\text{C}$ ) in temperature trial models and defined these parameters as fixed effects. Because we repeatedly measured many of the same birds at different temperatures in these trials, we used linear

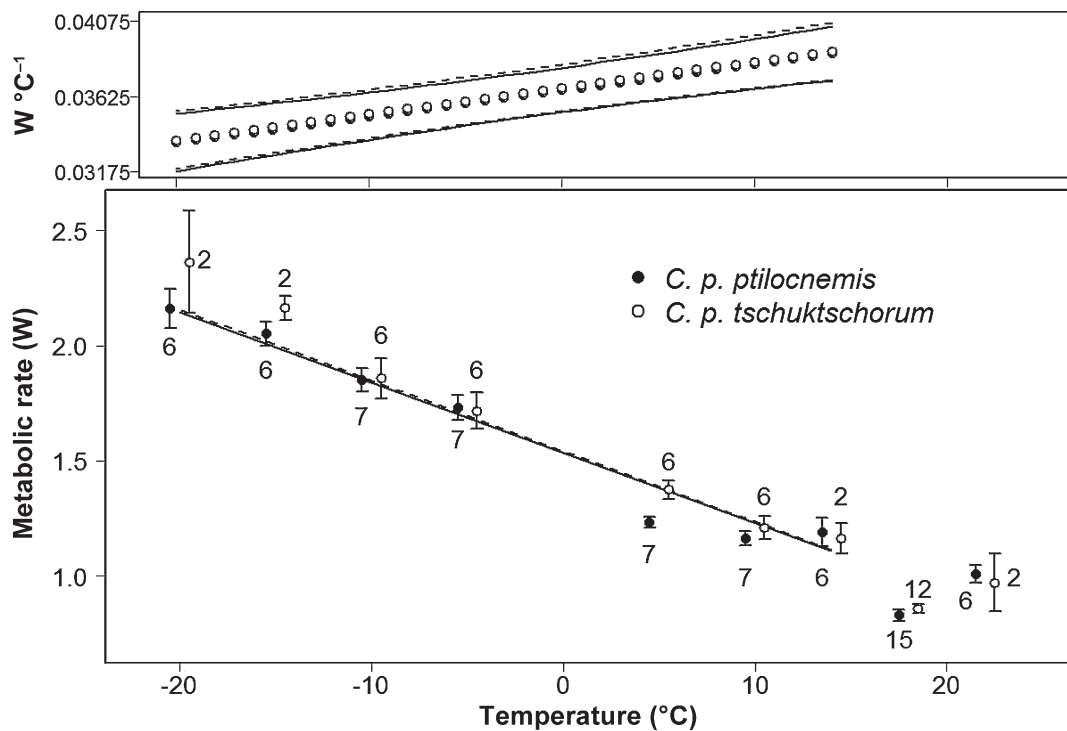


FIG. 1. Thermal conductance ( $W^{\circ}C^{-1}$ ; upper figure) and metabolic rate (W; lower figure) in response to temperature of *C. p. ptilocnemis* (filled symbols and solid lines) and *C. p. tschuktschorum* (open symbols and dashed lines). For conductance, plot shows model-averaged predictions  $\pm$  95% confidence intervals; for metabolic rate, symbols represent measured mean  $\pm$  SE, lines represent model-averaged predictions, and numbers represent sample size. Values in lower figure are offset from actual predictive temperatures for clarity.

mixed-effects models to account for random variation attributable to individual birds and modeled the individual birds as a random effect. To determine the most parsimonious modeling approach, we followed procedures outlined in Zuur et al. (2009) and compared three fully parameterized mixed-effects models that differed only in the correlation structure of the random effect component. This comparison consisted of a model with the random effect modeled as a simple scalar effect, a model fitting the random effect correlated to the level of temperature, and a model defining the random effect as scalar but uncorrelated to the level of temperature. Defining the random variation attributable to individual birds as a simple scalar effect was the most parsimonious approach, and we defined the random effect as such in all temperature models.

Measures of conductance in Red Knots indicated that birds became hypothermic only as low temperatures induced a metabolic response  $\sim 5 \times$  BMR (Vézina et al. 2006). Because metabolic outputs in Rock Sandpipers at  $-20^{\circ}C$  only approached  $\sim 2.5 \times$  BMR (see below), we assumed that birds were normothermic at all temperatures during temperature trials. There was little individual variation in the body temperature of Rock Sandpipers (mean  $\pm$  SE] cloacal temperature measured in thermoneutral environment =  $42.6 \pm 0.13^{\circ}C$ ;  $n = 8$  individuals). We calculated each bird's thermal conductance at experimental temperatures  $t \leq 14^{\circ}C$  using the formula (metabolic rate <sub>$t$</sub>  / [temperature<sub>body</sub> - temperature <sub>$t$</sub> ]; Piersma et al. 1995). We used the same model set as in the temperature analysis (see below). The results of the two analyses were nearly identical (the same three models in nearly equal proportions accounted for  $\sim 80\%$  of the entire model weight

in both analyses), and we report only model-averaged parameters and plot model-averaged predictions from the conductance analysis to avoid redundancy.

We followed the multimodel information-theoretic analytical approach outlined in Burnham and Anderson (2002) to examine support for our hypotheses about factors affecting the metabolic rate of Rock Sandpipers. For each analysis, we included different biologically relevant combinations of the explanatory variables. On the basis of results of previous studies, we included body mass in all our BMR models to control for size-related variation in metabolic rates (Packard and Boardman 1999), and temperature in all the mixed-effects models assessing the metabolic response to temperature (Scholander et al. 1950a, Scholander 1955). We compared five models in the BMR analysis and six models in the analyses of metabolic response to temperature and conductance (Table 2). We gauged support for each model using Akaike's information criterion adjusted for small sample size ( $AIC_c$ ) and based model inference on Akaike weights ( $w_i$ ; Burnham and Anderson 2002). We averaged our model results in proportion to Akaike weights to generate overall parameter and prediction estimates and considered parameters to be biologically meaningful if their model-averaged 95% confidence intervals did not overlap zero. We conducted all analyses in R, version 2.12.2, and fitted generalized linear models for the BMR analysis using the stats package (R Development Core Team 2011), mixed-effects models for the temperature and thermal conductance analyses using the lme4 package (Bates et al. 2011), and averaged model outputs using the AICcmodavg package (Mazerolle 2011). Estimates are presented as means  $\pm$  SE.



TABLE 2. Model rankings describing metabolic outputs of Rock Sandpipers. We fitted generalized linear models for the basal metabolic rate (BMR) trials, and linear mixed-effects models for the metabolic response to temperature trials. For BMR models, the number of parameters ( $k$ ) includes +1 $k$  for an intercept and +1 $k$  for residual estimate. For temperature models, in addition to +2 $k$  for intercept and residual term, +1 $k$  is added to each model, representing the random effect attributable to individual birds. We also applied the temperature models to the analysis of thermal conductance; see text for conductance model summaries.

BMR				Temperature			
Model <sup>a</sup>	$k$	$\Delta AIC_c^b$	$w_i$	Model <sup>a</sup>	$k$	$\Delta AIC_c^c$	$w_i$
Intercept	2	0.00	0.37	T	4	0.00	0.33
M	3	0.08	0.35	T + SX + M	6	0.13	0.31
SUB + M	4	1.99	0.14	T + M	5	1.43	0.16
SX + M	4	2.48	0.11	T + SX + SUB + M	7	2.06	0.12
SX + SUB + M	5	4.69	0.04	T + SUB + M	6	3.06	0.07
				Intercept	3	175.51	0.00

<sup>a</sup> M = mass, T = temperature, SUB = subspecies, and SX = sex.

<sup>b</sup> The lowest  $AIC_c$  score in the analysis was –53.10.

<sup>c</sup> The lowest  $AIC_c$  score in the analysis was –96.59.

## RESULTS

**Basal metabolic rate.**—Body mass of the sexes was similar between subspecies; females ( $90.2 \pm 3.3$  g for *ptilocnemis* and  $90.5 \pm 2.3$  g for *tshuktschorum*) weighed ~6% more than males ( $85.5 \pm 2.6$  g for *ptilocnemis* and  $84.0 \pm 3.5$  g for *tshuktschorum*).

The model selection process demonstrated limited support for the effect of body mass in predicting Rock Sandpiper BMR, and poor support for the other explanatory variables (Table 2). Model ranking indicated that the intercept-only model and a model with just body mass as an explanatory variable were nearly equally supported and together accounted for almost three-quarters of the overall model support ( $\Sigma w_i = 0.72$ ; Table 2). Models that included the effect of subspecies and sex were not well supported ( $\Sigma w_i = 0.18$  and  $\Sigma w_i = 0.15$ , respectively; Table 2), which indicates that these variables were not useful in predicting BMR. This was corroborated by the 95% confidence intervals of the parameter coefficients overlapping zero for subspecies, sex, and body mass (despite its inclusion in the second-most-supported model; Table 3).

We calculated the model-averaged estimates of BMR for each sex of each subspecies using the pertinent mean body mass values reported above, and these values were nearly identical. The estimated BMR for both *ptilocnemis* and *tshuktschorum* females was  $0.85 \pm 0.02$  W, and values for male *ptilocnemis* and *tshuktschorum* were  $0.83 \pm 0.02$  W and  $0.84 \pm 0.02$  W, respectively. These model-averaged predictions closely matched the mean values recorded during the actual trials for each sex of each subspecies (Fig. 2).

**Metabolic response to temperature.**—As with the BMR trials, females ( $91.1 \pm 3.0$  g for *ptilocnemis* and  $92.3 \pm 1.8$  g for *tshuktschorum*) weighed more (~4%) than males ( $89.2 \pm 2.1$  g for *ptilocnemis* and  $85.2 \pm 2.8$  g for *tshuktschorum*). The lower critical temperature for both subspecies fell between 14°C and 18°C (Fig. 1). We measured the metabolic rate of Rock Sandpipers at one temperature >18°C, and this trial indicated that the upper critical temperature for each subspecies was between 18°C and 22°C (Fig. 1). Thus, the exact upper and lower critical temperatures are unknown, but the thermoneutral zone for both subspecies most likely falls between 14°C and 22°C.

The metabolic rate of Rock Sandpipers increased at temperatures below the thermoneutral zone (Fig. 1). The model-averaged regression lines for each subspecies climbed with essentially equal slopes and intercepts as temperatures declined (Fig. 1). The best-supported model included the effects of temperature alone, and this model accounted for one-third of the total model weight (Table 2). As with the BMR analysis, the effects of body mass, sex, and subspecies were minimal: all the model-averaged 95% confidence intervals for these variables overlapped zero (Table 3). The combined model weight for models that included temperature was 1.00, but models that included body mass ( $\Sigma w_i = 0.66$ ), sex ( $\Sigma w_i = 0.43$ ), and subspecies ( $\Sigma w_i = 0.19$ ) were not as well supported, and there was essentially no support for the intercept-only model (Table 2). Temperature was also the only predictor variable with 95% confidence intervals that did not overlap zero (Table 3). The model-averaged parameter estimate for temperature was –0.03, indicating an increase in metabolic rate of 0.03 W for each 1°C drop in temperature below 14°C.

**Thermal conductance.**—Our analysis of variation in conductance compared the same six models used in the temperature analysis (Table 2). As with the temperature trials, the best-supported model contained only temperature, and this model accounted for one-third of the total model weight ( $w_i =$

TABLE 3. Model-averaged parameter estimates (with 95% confidence intervals in parentheses) for factors predicting the metabolic output (W) and conductance ( $W\ ^\circ C^{-1}$ ) of Rock Sandpipers. Results are from basal metabolic rate (BMR), metabolic response to temperature below the thermoneutral zone (Temperature), and conductance models presented in Table 2.

BMR (W)		Temperature (W)		Conductance ( $W\ ^\circ C^{-1}$ )	
Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
Mass	0.002 (–0.001 to 0.005)	Mass	–0.002 (–0.006 to 0.002)	Mass	–0.00006 (–0.0002 to 0.00004)
Sex <sup>a</sup>	–0.003 (–0.015 to 0.009)	Sex <sup>a</sup>	–0.044 (–0.111 to 0.023)	Sex <sup>a</sup>	–0.001 (–0.003 to 0.001)
Subspecies <sup>b</sup>	–0.005 (–0.019 to 0.009)	Subspecies <sup>b</sup>	–0.008 (–0.031 to 0.016)	Subspecies <sup>b</sup>	0.00001 (–0.0004 to 0.0004)
Intercept	0.679 (0.278 to 1.080)	Temperature	–0.030 (–0.033 to –0.028)	Temperature	0.00015 (0.0001 to 0.0002)
		Intercept	1.729 (1.228 to 2.231)	Intercept	0.043 (0.029 to 0.056)

<sup>a</sup> Males are the reference level.

<sup>b</sup> *Calidris ptilocnemis ptilocnemis* is the reference level.

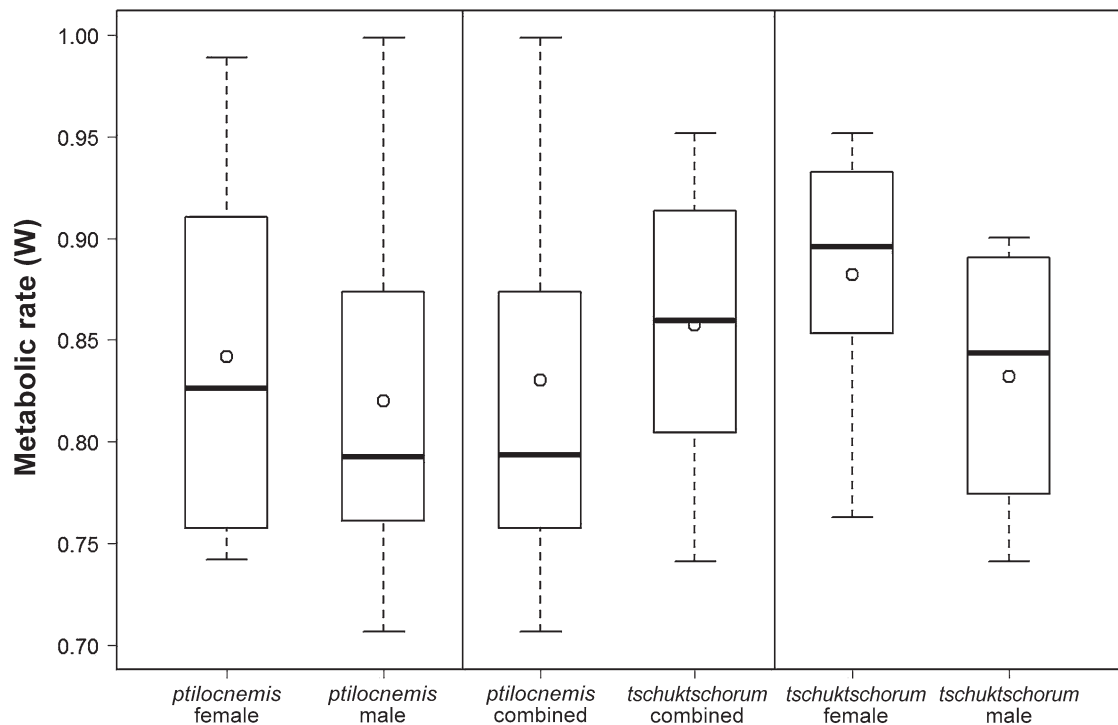


FIG. 2. Measured basal metabolic rates (W) of Rock Sandpipers by sex and subspecies. Horizontal line represents median, circle the mean, box the 25th and 75th percentiles, and whiskers the range of values.

0.34). Models that included temperature, sex, and body mass ( $w_i = 0.32$ ) or temperature and body mass ( $w_i = 0.19$ ) were also well supported, but temperature was the only predictor variable whose 95% confidence interval did not overlap zero (Table 3). Model-averaged estimates of conductance decreased slightly with decreasing temperatures in both subspecies (Fig. 1). Applying trial-specific mean body masses, the model-averaged estimates of conductance across our range of predictive temperatures were equal for *ptilocnemis* and *tschuktschorum* females ( $0.039 \pm 0.001 \text{ W } ^\circ\text{C}^{-1}$  and  $0.034 \pm 0.001 \text{ W } ^\circ\text{C}^{-1}$  at  $14^\circ\text{C}$  and  $-20^\circ\text{C}$ , respectively), and differed little from males ( $0.038 \pm 0.001 \text{ W } ^\circ\text{C}^{-1}$  and  $0.039 \pm 0.001 \text{ W } ^\circ\text{C}^{-1}$  for *ptilocnemis* and *tschuktschorum* males at  $14^\circ\text{C}$ ; both subspecies  $0.033 \pm 0.001 \text{ W } ^\circ\text{C}^{-1}$  at  $-20^\circ\text{C}$ ). Minimal thermal conductance occurred at lower rather than higher temperatures below the thermoneutral zone.

## DISCUSSION

In contrast to previous studies that documented metabolic differences between closely related study groups (e.g., Niewiarowski and Roosenburg 1993; Klaassen 1995; Mueller and Diamond 2001; Wikelski et al. 2003; Broggi et al. 2004, 2005; Tieleman 2007), we found no evidence of intrinsic differences in basic metabolic parameters between *C. p. ptilocnemis* and *C. p. tschuktschorum* held under identical conditions. There was no variation in BMR or thermal conductance of Rock Sandpipers by sex or subspecies, and the metabolic response of each subspecies to temperature did not differ. Given their more northerly nonbreeding distribution and exposure to colder temperatures, we reasoned that the plumage of *ptilocnemis* would differ from

and provide more insulation than the plumage of *tschuktschorum* (e.g., Blem 1981, Piersma et al. 1995), but this was not the case and suggests that the two subspecies derive similar insulation from their plumages.

Although the two subspecies did not differ with respect to these basic metabolic parameters, Rock Sandpipers appear to exhibit unique adaptations to cold environments compared with birds in general. For instance, our measures of BMR did not diverge from expected patterns in shorebirds based on body mass. Substituting the mean body mass of each sex of each subspecies measured during the BMR trials in the shorebird-specific equation derived by Kersten and Piersma (1987) yields BMR estimates for males and females of both subspecies that are within 1–3% of our model-averaged estimates. Our model-averaged estimates of thermal conductance, however, were lower than predicted, and this difference may reflect adaptations to colder environments. Applying trial-specific body masses to equation 8-15 in Calder (1996) yielded estimates of minimal conductance ~10% higher than our model-averaged estimates of thermal conductance at  $-20^\circ\text{C}$  for both subspecies.

Thermal conductance in both subspecies declined slightly at the lowest environmental temperatures (Fig. 1), a phenomenon commonly encountered as animals allow slight drops in their body temperature and/or combine physical and chemical thermoregulation processes at low temperatures (McNab 1980). Additionally, comparisons with other shorebirds show that the model-averaged intercept and slope estimates for temperature are smaller for Rock Sandpipers than for species with more temperate nonbreeding ranges assessed by Kersten and Piersma (1987). Because the intercept term in these models is primarily a function of body mass, the smaller value for Rock Sandpipers is simply a reflection of their

smaller mass compared with the larger shorebird species measured by Kersten and Piersma (1987). The model-averaged slope parameter for temperature, however, is 1.5–3.3 times smaller for Rock Sandpipers, indicating that their metabolic rates increase relatively less as temperatures decrease below their thermoneutral zone than in other shorebird species. Thus, thermal conductance values are lower than predicted and the metabolic response to temperature is more moderate in Rock Sandpipers, which may represent intrinsic, genetically fixed adaptations to their year-round existence at thermally demanding high-latitude sites. Potential adaptations that may account for these observed deviations from predictions include increased plumage insulation (Dawson and Carey 1976, Swanson 1991), behavioral adaptations (e.g., ptiloerection, Hohtola et al. 1980; shivering thermogenesis, Hohtola 2004), and various nonshivering processes (e.g., chemical thermoregulation; Dawson and O'Connor 1996, Vézina et al. 2011).

Although environmental conditions across their nonbreeding ranges undoubtedly induce different metabolic demands (Table 1), the range of demands was not reflected by inherent differences in basic metabolic parameters in the two subspecies. In a similar comparison, the BMR of wild Red Knots of the northerly-wintering *islandica* subspecies was greater than that of tropical-wintering *canutus* (Piersma et al. 1996a), but these measures equalized in captivity when the two subspecies were maintained under identical conditions (Piersma et al. 1996a). Red Knots exhibit a wide range of metabolic response to temperature, and these responses are dictated by acclimatization to prevailing environmental conditions (Vézina et al. 2006, 2007, 2011). The BMR of cold-acclimated Red Knots was 26% higher than that of warm-acclimated Red Knots (Vézina et al. 2006), and cold-acclimated birds exhibited greater cold tolerance and had higher summit metabolic rates than warm-acclimated birds (Vézina et al. 2006). These results demonstrate the degree to which BMR is phenotypically modulated in migratory shorebirds. Given the predicted differences in metabolic rates of wild Rock Sandpipers (Table 1) and the equality of values when held identically in captivity, our results likewise suggest that we measured metabolic outputs of identically acclimatized birds across a range of conditions within the phenotypic breadth of each subspecies.

The thermal environments at the extremes of the two subspecies' nonbreeding ranges appear to be very different (i.e., upper Cook Inlet and Humboldt Bay; Table 1), but to a species adapted to the climatic extremes of high-northern latitudes such differences may not be sufficiently strong to induce a detectable metabolic response. Like other high-latitude breeding shorebirds, the two Rock Sandpiper subspecies that we studied must contend with a wide array of environmental conditions throughout their annual cycle (Wiersma and Piersma 1994, Piersma 2002), likely inducing selection for phenotypic flexibility in metabolic output (Kersten and Piersma 1987, Piersma et al. 1995, Piersma 2002). Our initial belief was that strongly contrasting winter conditions would induce fixed metabolic differences between the subspecies, but, as with other shorebird species, it is instead probable that a wide range of cross-seasonal environmental conditions more strongly regulates the metabolic output of Rock Sandpipers (Piersma 1996).

Given the equality of the two subspecies' metabolic capacities, it is likely that ecological factors more strongly determine their nonbreeding distributions. Rock Sandpiper nonbreeding distributions are influenced by myriad biotic and abiotic interactions (e.g., predator abundance, storm severity and duration, food abundance, day

length, wind speed, and fasting endurance), and metabolic capacities are undoubtedly just part of the complex process that regulates their distributions. For instance, van Gils et al. (2004, 2005b) demonstrated that the distribution of Red Knots in the Dutch Wadden Sea is primarily explained by the abundance, quality, and digestibility of their prey and the interaction of these prey characteristics with phenotypically flexible body components like gizzard size. For free-living *ptilocnemis* Rock Sandpipers, acclimatization to low temperatures likely promotes the higher metabolic outputs necessary to occupy upper Cook Inlet during winter. Because of the high energetic demands of wintering at this site (Table 1), foraging-related adaptations likely also support their unique nonbreeding distribution. For example, individuals of the *ptilocnemis* subspecies forage exclusively on mudflats in upper Cook Inlet whereas individuals of the *tschuktschorum* subspecies primarily forage on rocky intertidal substrates (Gill et al. 2002), and these habitat preferences are reflected in the two subspecies' winter plumages. The pale gray plumage of *ptilocnemis* provides crypsis on foraging substrates (mudflats) and roosting sites (sea ice and snow-covered shorelines), whereas *tschuktschorum*'s darker plumage blends to its preferred rocky shoreline habitat. Accordingly, their separate distributions may reflect subspecific differences in phenotypically conserved traits like plumage patterns. Given their discrete nonbreeding foraging-habitat preferences (mudflat vs. rocky intertidal), the two subspecies also likely exhibit different foraging ecologies (e.g., search efficiency, prey preferences, prey intake, and processing rates). In the absence of subspecific differences in basic metabolic traits, phenotypically mediated adaptations that allow Rock Sandpipers to safely and predictably satisfy their energetic requirements are instead the likely determinants of subspecific winter distributions.

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#### LITERATURE CITED

- BARTHOLOMEW, G. A. 1982. Body temperature and energy metabolism. Pages 333–406 in *Animal Physiology: Principles and Adaptations*, 4th ed. (M. S. Gordon, Ed.). Macmillan, New York.
- BATES, D., M. MAECHLER, AND B. BOLKER. 2011. lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 0.999375-39. [Online.] Available at [CRAN.R-project.org/package=lme4](http://CRAN.R-project.org/package=lme4).



- BATTLE, P. F., AND T. PIERSMA. 2005. Adaptive interplay between feeding ecology and features of the digestive tract in birds. Pages 201–228 in *Physiological and Ecological Adaptations to Feeding in Vertebrates* (J. M. Starck and T. Wang, Eds.). Science Publishers, Enfield, New Hampshire.
- BATTLE, P. F., N. WARNOCK, T. L. TIBBITTS, R. E. GILL, JR., T. PIERSMA, C. J. HASSELL, D. C. DOUGLAS, D. M. MULCAHY, B. D. GARTRELL, R. SCHUCKARD, AND OTHERS. 2012. Contrasting extreme long-distance migration patterns in Bar-tailed Godwits *Limosa lapponica*. *Journal of Avian Biology* 43:21–32.
- BLEM, C. R. 1981. Geographic variation in mid-winter body composition of starlings. *Condor* 83:370–376.
- BLEM, C. R. 1990. Avian energy storage. Pages 59–113 in *Current Ornithology*, vol. 7 (D. M. Power, Ed.). Plenum Press, New York.
- BROGGI, J., E. HOHTOLA, M. ORELL, AND J.-Å. NILSSON. 2005. Local adaptation to winter conditions in a passerine spreading north: A common-garden approach. *Evolution* 59:1600–1603.
- BROGGI, J., M. ORELL, E. HOHTOLA, AND J.-Å. NILSSON. 2004. Metabolic response to temperature variation in the Great Tit: An inter-population comparison. *Journal of Animal Ecology* 73:967–972.
- BUEHLER, D. M., AND A. J. BAKER. 2005. Population divergence times and historical demography in Red Knots and Dunlins. *Condor* 107:497–513.
- BUEHLER, D. M., B. I. TIELEMAN, AND T. PIERSMA. 2009. Age and environment affect constitutive immune function in Red Knots (*Calidris canutus*). *Journal of Ornithology* 150:815–825.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- CALDER, W. A., III. 1996. *Size, Function, and Life History*. Dover, Mineola, New York.
- CAREY, C., W. R. DAWSON, L. C. MAXWELL, AND J. A. FAULKNER. 1978. Seasonal acclimatization to temperature in cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. *Journal of Comparative Physiology B* 125:101–113.
- CASTRO, G. 1987. High basal metabolic rate in Sanderlings (*Calidris alba*). *Wilson Bulletin* 99:267–268.
- CONOVER, H. B. 1944. The North Pacific allies of the Purple Sandpiper. *Field Museum of Natural History Zoological Series* 29:169–179.
- COOPER, S. J. 2002. Seasonal metabolic acclimatization in Mountain Chickadees and Juniper Titmice. *Physiological and Biochemical Zoology* 75:386–395.
- DAWSON, W. R., AND C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. *Journal of Comparative Physiology B* 112:317–333.
- DAWSON, W. R., AND T. P. O'CONNOR. 1996. Energetic features of avian thermoregulatory responses. Pages 85–124 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.
- DUTENHOFFER, M. S., AND D. L. SWANSON. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology* 69:1232–1254.
- DYKSTRA, C. R., AND W. H. KARASOV. 1992. Changes in gut structure and function of House Wrens (*Troglodytes aedon*) in response to increased energy demands. *Physiological Zoology* 65:422–442.
- GESSAMAN, J. A., AND K. A. NAGY. 1988. Energy metabolism: Errors in gas-exchange conversion factors. *Physiological Zoology* 61:507–513.
- GILL, R. E., P. S. TOMKOVICH, AND B. J. MCCAFFERY. 2002. Rock Sandpiper (*Calidris ptilocnemis*). In *The Birds of North America*, no. 686 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- GRIFFITHS, R., S. DAAN, AND C. DIJKSTRA. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London, Series B* 263:1251–1256.
- HOHTOLA, E. 2004. Shivering thermogenesis in birds and mammals. Pages 241–252 in *Life in the Cold: Evolution, Mechanisms, Adaptation, and Application* (B. M. Barnes and H. V. Carey, Eds.). Institute of Arctic Biology, University of Alaska, Fairbanks.
- HOHTOLA, E., H. RINTAMÄKI, AND R. HISSA. 1980. Shivering and ptiloerection as complementary cold defense responses in the pigeon during sleep and wakefulness. *Journal of Comparative Physiology B* 136:77–81.
- IUPS THERMAL COMMISSION. 2003. Glossary of terms for thermal physiology. *Journal of Thermal Biology* 28:75–106.
- KARASOV, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology. Pages 61–84 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.
- KERSTEN, M., AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds: Metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175–187.
- KLAASSEN, M. 1995. Molt and basal metabolic costs in males of two subspecies of Stonechats: The European *Saxicola torquata rubicula* and the east African *S. t. axillaris*. *Oecologia* 104:424–432.
- MAZEROLLE, M. J. 2011. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.15. [Online.] Available at [CRAN.R-project.org/package=AICcmodavg](http://CRAN.R-project.org/package=AICcmodavg).
- MENAB, B. K. 1980. On estimating thermal conductance in endotherms. *Physiological Zoology* 53:145–156.
- MUELLER, P., AND J. DIAMOND. 2001. Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. *Proceedings of the National Academy of Sciences USA* 98:12550–12554.
- NATIONAL AERONAUTICS AND SPACE ADMINISTRATION. 2012. Surface meteorology and solar energy. [Online.] Available at [eosweb.larc.nasa.gov/sse/](http://eosweb.larc.nasa.gov/sse/).
- NIEMIAROWSKI, P. H., AND W. ROOSENBURG. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* 74:1992–2002.
- PACKARD, G. C., AND T. J. BOARDMAN. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: Wasted time, wasted effort? *Comparative Biochemistry and Physiology A* 122:37–44.
- PIERSMA, T. 1996. Energetic constraints on the non-breeding distribution of coastal shorebirds. *International Wader Studies* 8:122–135.
- PIERSMA, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. *Integrative and Comparative Biology* 42:51–67.
- PIERSMA, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology* 148:S45–S59.
- PIERSMA, T. 2011. Why marathon migrants get away with high metabolic ceilings: Towards an ecology of physiological restraint. *Journal of Experimental Biology* 214:295–302.
- PIERSMA, T., L. BRUNZEEL, R. DRENT, M. KERSTEN, J. VAN DER MEER, AND P. WIERSMA. 1996a. Variability in basal metabolic rate

- of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* 69:191–217.
- PIERSMA, T., N. CADÉE, AND S. DAAN. 1995. Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the knot (*Calidris canutus*). *Journal of Comparative Physiology B* 165:37–45.
- PIERSMA, T., J. A. GESSAMAN, A. DEKINGA, AND G. H. VISSER. 2004. Gizzard and other lean mass components increase, yet basal metabolic rates decrease, when Red Knots *Calidris canutus* are shifted from soft to hard-shelled food. *Journal of Avian Biology* 35:99–104.
- PIERSMA, T., AND Å. LINDSTRÖM. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology & Evolution* 12:134–138.
- PIERSMA, T., AND J. A. VAN GILS. 2011. *The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford University Press, Oxford.
- PIERSMA, T., J. A. VAN GILS, AND P. WIERSMA. 1996b. Family Scolopacidae (sandpipers, snipes, and phalaropes). Pages 444–533 in *Handbook of the Birds of the World*, vol. 3: Hoatzin to Auks (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- PITELKA, F. A., R. T. HOLMES, AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in Arctic sandpipers. *American Zoologist* 14:185–204.
- PRUETT, C. L., AND K. WINKER. 2005. Biological impacts of climatic change on a Beringian endemic: Cryptic refugia in the establishment and differentiation of the Rock Sandpiper (*Calidris ptilocnemis*). *Climatic Change* 68:219–240.
- R DEVELOPMENT CORE TEAM. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- REZENDE, E. L., D. L. SWANSON, F. F. NOVOA, AND F. BOZINOVIC. 2002. Passerines versus nonpasserines: So far, no statistical differences in the scaling of avian energetics. *Journal of Experimental Biology* 205:101–107.
- RUTHRAUFF, D. R., R. E. GILL, JR., AND T. L. TIBBITTS. 2013. Coping with the cold: An ecological context for the abundance and distribution of Rock Sandpipers during winter in upper Cook Inlet, Alaska. *Arctic* 66: *in press*.
- SCHOLANDER, P. F. 1955. Evolution of climatic adaptation in homeotherms. *Evolution* 9:15–26.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, AND L. IRVING. 1950a. Adaptation to cold in Arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin* 99:259–271.
- SCHOLANDER, P. F., V. WALTERS, R. HOCK, AND L. IRVING. 1950b. Body insulation of some Arctic and tropical mammals and birds. *Biological Bulletin* 99:225–236.
- STEARNS, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- SWANSON, D. L. 1991. Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. *Condor* 93:538–545.
- SWANSON, D. L. 2010. Seasonal metabolic variation in birds: Functional and mechanistic correlates. Pages 75–129 in *Current Ornithology*, vol. 17 (C. F. Thompson, Ed.). Plenum Press, New York.
- TIELEMAN, B. I. 2007. Differences in the physiological responses to temperature among Stonechats from three populations reared in a common environment. *Comparative Biochemistry and Physiology A* 146:194–199.
- U.S. NAVAL OBSERVATORY. 2012. Duration of daylight/darkness table for one year. [Online.] Available at [aa.usno.navy.mil/data/docs/Dur\\_OneYear.php](http://aa.usno.navy.mil/data/docs/Dur_OneYear.php).
- VAN GILS, J. A., P. F. BATTLEY, T. PIERSMA, AND R. DRENT. 2005a. Reinterpretation of gizzard sizes of Red Knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proceedings of the Royal Society of London, Series B* 272:2609–2618.
- VAN GILS, J. A., A. DEKINGA, B. SPAANS, W. K. VAHL, AND T. PIERSMA. 2005b. Digestive bottleneck affects foraging decisions in Red Knots *Calidris canutus*. II. Patch choice and length of working day. *Journal of Animal Ecology* 74:120–130.
- VAN GILS, J. A., S. R. DE ROOIJ, J. VAN BELLE, J. VAN DER MEER, A. DEKINGA, T. PIERSMA, AND R. DRENT. 2004. Digestive bottleneck affects foraging decisions in Red Knots *Calidris canutus*. I. Prey choice. *Journal of Animal Ecology* 74:105–119.
- VÉZINA, F., A. DEKINGA, AND T. PIERSMA. 2011. Shorebirds' seasonal adjustments in thermogenic capacity are reflected by changes in body mass: How preprogrammed and instantaneous acclimation work together. *Integrative and Comparative Biology* 51:394–408.
- VÉZINA, F., A. GUSTOWSKA, K. M. JALVINGH, O. CHASTEL, AND T. PIERSMA. 2009. Hormonal correlates and thermoregulatory consequences of molting on metabolic rate in a northerly wintering shorebird. *Physiological and Biochemical Zoology* 82: 129–142.
- VÉZINA, F., K. M. JALVINGH, A. DEKINGA, AND T. PIERSMA. 2006. Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. *Journal of Experimental Biology* 209:3141–3154.
- VÉZINA, F., K. M. JALVINGH, A. DEKINGA, AND T. PIERSMA. 2007. Thermogenic side effects to migratory predisposition in shorebirds. *American Journal of Physiology* 292:R1287–R1297.
- WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia* 42:81–89.
- WEST, G. C. 1972. Seasonal differences in resting metabolic rate of Alaskan ptarmigan. *Comparative Biochemistry and Physiology A* 42:867–876.
- WESTERN REGIONAL CLIMATE CENTER. 2012. Historical climate information station data inventories. [Online.] Available at [www.wrcc.dri.edu/](http://www.wrcc.dri.edu/).
- WHITE, C. M., AND G. C. WEST. 1977. The annual lipid cycle and feeding behavior of Alaskan redpolls. *Oecologia* 27:227–238.
- WIERSMA, P., AND T. PIERSMA. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. *Condor* 96:257–279.
- WIKELSKI, M., L. SPINNEY, W. SCHELSKY, A. SCHEUERLEIN, AND E. GWINNER. 2003. Slow pace of life in tropical sedentary birds: A common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London, Series B* 270:2383–2388.
- WILLIAMS, J. B., A. MUÑOZ-GARCIA, S. OSTROWSKI, AND B. I. TIELEMAN. 2004. A phylogenetic analysis of basal metabolism, total evaporative water loss, and life-history among foxes from desert and mesic regions. *Journal of Comparative Physiology B* 174:29–39.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.